STUDIES ON AUSTRALIAN CAINOZOIC BRACHIOPODS

3. The Subfamily Bouchardiinae (Terebratellidae)

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ABSTRACT: The Australian Tertiary species *Malleia portlandica* (Chapman 1913) is re-described and *Malleia* is transferred from the Neothyrinae to the Bourchardiinae. The Bouchardiinae and the monotypic genera *Malleia* and *Neoboucliardia* are all re-defined.

INTRODUCTION

A revision of Australian Cainozoic brachiopods is in progress and, for comparative purposes, Mesozoic and New Zealand genera are being examined wherever possible. This work is concerned with the structures which are of prime importance in classification, namely the developmental and adult patterns of the loop, and adult patterns of the cardinalia. The bulk of material available is attributable to the family Terebratellidae which is composed, almost exclusively, of austral forms. The classification of the family is so unwieldy that it is desirable for the genera to be re-arranged in more workable subfamily groupings indicating, if not true phyletic relationships, at least some more coherent picture of apparent similarities.

The subfamily Bouchardiinae is represented in Australia by two species, *Neoboucliardia minima* (Thomson 1918) from the Oligocene of Victoria and *Bouchardiella cretacea* Etheridge (1913) from Upper Cretaceous beds of Western Australia, and it is proposed that the genus *Malleia* be transferred to the Bouchardiinae from the Neothyrinae. To place *Malleia* in the Bouchardiinae involves changing the diagnosis of both the subfamily Bouchardiinae and the genus *Malleia*. For it is proposed that, to a group of genera which agree in foramen position (epithyrid), type of deltidial plate (fused, not delimited within the palintrope) and in the possession of a solid hinge platform without hinge trough or bifurcating septum, a genus be added with a hypothyrid foramen, discrete deltidial plates and alleged by Thomson (1927) and Allan (1940) to possess a hinge trough and a bifurcating septum.

That the four genera now assigned to this subfamily form a related group is suggested by the number of features which they bear in common, and which are also unique to the subfamily i.e. cardinalia consisting of socket ridges and a cardinal process of distinctive shape, a high median septum which does not unite with the cardinalia, and no loop. Those features in which they differ (foraminal position, type of deltidial plate, extent of thickening of cardinalia) seem to be related to the loss of the supportive function of the pedicle and are not considered to be of significance at the subfamily level.

Subfamily BOUCHARDIINAE Allan, 1940
Emend. nov.

DIAGNOSIS: Terebratellidae with cardinalia consisting of socket ridges and a cardinal process; with a high median septum which may bear lamellae and which is not connected with the cardinalia; with sulcate folding, hypothyrid or epithyrid foramina and discrete or fused deltidial plates.

KEY TO GENERA

Foramen hypothyrid, deltidial plates
discrete, socket ridges and cardinal
process defined . . . . *Malleia*
Foramen minute and epithyrid, delti-
dial plates fused and not delimited
within the palintrope, cardinalia
fused into solid platform:
  1. anterior rim of cardinal pro-
     cess fully indented . . . . . *Bouchardia*
  2. anterior rim of cardinal pro-
     cess partially indented:
     a. lamellae on septum . . . . *Bouchardiella*
     b. boss on septum . . . . . . *Neobouchardia*

DISCUSSION: Allan (1940) created the subfamily Bouchardiinae for three genera (*Bouchardiella, Bouchardia, Neobouchardia*) which Thomson (1927, p. 271) had noted 'present certain characters in common which sharply distinguished them from other rostrate Telotremata'. Allan's diagnosis, which was adopted by Hatai and Elliott (1965), states that in

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these genera 'the crural bases unite in a hinge-platform, the septum is unbifurcated, there is no hinge-trough' (p. 270).

In the present paper, the monotypic genus *Malleia* is transferred from the subfamily Neothyridinae to the Bouchardiinae. *Malleia* was assigned by Allan (1940) to the Neothyrinae on the basis of a broadly bifurcating septum and a long, broad hinge trough. A subsequent paper will discuss forms exhibiting hinge plates in association with an apparently bifurcating septum. Hinge plates are not present in *Malleia*, nor does the septum bifurcate. As described in detail for *Malleia portlandica* (Chapman 1913), the floor of the dorsal valve bears oblique ridges extending from the bases of the socket ridges to the mid-line of the valve. These ridges give the appearance of marking the posterior limits of the adductor muscle scars in those specimens in which the scars are well defined (Pl. 7, fig. 6). Also in many specimens the low ridge marking the posterior limit of the median septum extends further posteriorly than the posterior limits of these ridges. Since the median septum of *Malleia* does not bifurcate and furthermore does not unite with the cardinalia, that area of the shell previously termed the 'hinge trough' is merely the posterior floor of the dorsal valve which is continuous with a cavity or cave underlying the cardinal process.

The Bouchardiinae display a solid hinge platform which apparently consists of thick socket ridges fused with a large cardinal process. It is difficult to describe the cardinal processes seen in the Terebratellidae without distinguishing the anterior and posterior surfaces indentified by Thomson (1927) but not defined in the Treatise (1965). Consequently the following definition is included herein.

The cardinal process is a median unpaired process lying at the posterior end of the interior of the dorsal valve and serves for the attachment of the dorsal ends of the diductor muscles. The cardinal process commonly displays two different types of surface—a flattened (or concave), striated (or roughened) surface and a smooth, commonly convex, surface. The striated surface faces ventrally and, to a varying degree, posteriorly and is termed the **posterior surface**. *The smooth surface, termed the* **anterior surface**, *may extend below the posterior surface and thus face dorsally or it may be expanded to form a conical or globular process facing largely anteriorly. The rim of the cardinal process is the line of junction of the anterior and posterior surfaces.*

Thomson (1927, p. 88) defines a *transverse* cardinal process as one which is broader than long and in which the striated or roughened surface is most prominent and faces nearly ventrally.

The cardinal process of the Bouchardiinae is unlike that seen in any other members of the Terebratellidae (Pl. 7, fig. 2, 6-8). It is most easily described as the derivative of a shallow, rimmed bowl with an inner, roughened concave surface representing the posterior surface and an outer smooth, convex surface representing the anterior surface of the cardinal process. The anterior rim of this bowl now becomes indented medially and moves posteriorly to fuse with the medial region of the posterior rim thus presenting the surface appearance of two lateral pockets on either side of a median indentation. The lateral pockets extend obliquely from the median posterior region of the cardinal process thus giving the inverted V-shaped appearance to the cardinal process described by Davidson (1887, p. 116) and Thomson (1927, p. 273). The cardinal process of *Neobouchardia* shows the first stage of folding (i.e. the median indentation of the anterior rim) which culminates in the complete fusion of the anterior and posterior rims of the cardinal processes in *Bouchardia* and *Malleia*. In *Bouchardia* the posterior regions of both valves are greatly thickened and the cardinal process is fused with the floor of the valve; the cardinal process of *Malleia* does not fuse with the dorsal valve floor and the cavity underlying it is continuous anteriorly with the remainder of the valve floor. These cavities or caves underlying regions of the cardinalia are a characteristic feature of the Bouchardiinae and their extent is governed by the amount of secondary thickening which has occurred in the posterior segment of the dorsal valve. Thus in *Malleia* one large cave is delimited posteriorly by the dorsal umbo region, laterally by the socket ridges and ventrally by the dorsal surface of the cardinal process. In the remaining three genera the anterior surface of the base of the hinge platform is marked by two or more shallow caves.

In his diagnosis of the subfamily Allan (1940, p. 270) states that 'the crural bases unite in a hinge platform'. Neither crural bases nor crura are recognizable in *Malleia* nor have they been described in any of the species attributed to the remaining three genera of the Bouchardiinae. It is possible that crural bases are present but are so intimately fused with other elements of the cardinalia that they are unidentifiable as separate structures. However, until the study of youthful forms of any of the species demonstrates their presence and later fusion with other elements, it seems inadvisable to describe the presence of crural bases as characteristic of the Bouchardiinae. Since none of the genera attributed to the Bouchardiinae are described as possessing crura, the existence of crural bases seems unlikely.

None of the species attributed to the Bouchardiinae possesses a loop: they all display a high plate-like median septum which tapers off abruptly posteriorly and does not unite with the cardinalia. The genera vary in the type of structure attached to the septum. In *Neobouchardia* a small swollen boss lies on the posterior end of the elevated part of the septum. *Bouchardia* and *Bouchardiella* are characterized by curved lamellae, which do not unite, extending from the septum. There are no descending branches apparent in these genera. The septum of *Malleia* exhibits curved lamellae, similar to those of *Bouchardia* and *Bouchardiella*, and, between these lamellae and the valve floor, small triangular plates extend from the septum representing either the rudiments or the only portions remaining of descending branches. A noteworthy feature of the curved lamellae of *Malleia* is their position on the septum. The oblique lines of attachment of the lamellae extend, not from the lateral margins of the

crest of the septum as is characteristic of other members of the Terebratellidae but from the sides of the septum at its approximate mid-height. Elliott (1952) describes the curved lamella of *Bouchardiella cretacea* as arising just below the summit of the septum and the same condition seems to be characteristic of *Bouchardia rosea* as described by Davidson (1850, 1887).

Some comment upon *Bouchardiella cretacea* in relation to other members of the Bouchardiinae is appropriate. *Bouchardiella patagonica* (Ihering 1903), the type species, is not well documented and is stated (Doello-Jurado 1922, p. 200) to differ from *Bouchardia* only in the less advanced cardinal process, a feature which Thomson (1927) regarded as hardly worthy of generic rank. Neither specimens nor figures of *B. patagonica* have been examined either by the writer or by Elliott who emended the diagnosis of the genus (1965) to include *B. cretacea* from Upper Cretaceous beds of Western Australia. Elliott (1952) describes the posterior surface of the cardinal process of *B. cretacea* as a shallow, heart-shaped muscle-pit with anterior indentation. From his description the cardinal process seemed similar to that of *Neobouchardia*. However, judging from topotypes the cardinal process is almost identical with that of *Magadina cumingi* (Davidson 1852). In all other feaures *B. cretacea* is closely related to other members of the Bouchardiinae and as Elliott states 'appears to be a form very near the ancestral junction of the Bouchardiinae and Magasinae' (1952, p. 13).

Two factors appear to be responsible for the morphological features characteristic of the Bouchardiinae. First, as a result of possessing only early ontogenetic loop structures (the structures giving rise to the adult loop in other terebratellids) two bourchardiform features must follow i.e. the septum is not associated with the cardinalia and, in the absence of crura, crural bases are not apparent. In other subfamilies of the Terebratellidae crural bases and sometimes hinge plates contribute to the hinge platform in addition to the socket ridges and the cardinal process. The absence of these additional elements of the cardinalia is probably the reason for the presence of caves in areas of the hinge platform. The second factor is that all members of the Bouchardiinae, with the exception of *Malleia*, display great thickening of the posterior regions of both valves. This condition allied with the presence of a tiny foramen occurs in many brachiopods and has been discussed by Rudwick (1970). He points out that posterior weighting of the shell can maintain its stability, that this may occur even in shells with a functional pedicle, but that its importance, and the extent of weighting, increases as the pedicle becomes reduced and can fulfil only a tethering function. Atrophy of the pedicle and foramen implies a free-lying habit and reliance on posterior weighting as a shell stabilizer.

In the course of these studies a number of Cainozoic brachiopods from different families have been examined and the presence of a small or atrophied foramen is associated invariably with great thickening in the posterior regions of the valves. The absence of excessive thickening in *Malleia* is related to the other features in which this genus differs from the remaining members of the subfamily i.e. the easier identification of the components of the cardinalia, a foramen of functional size, discrete deltidial plates and perhaps the more extensive development of septal structures.

From three dried specimens (from Zanzibar and the Gulf of Aden) Muir-Wood (1959) described the new genus and species *Leptothyris ignota* (now *Leptothyrella* as *Leptothyris* is preoccupied). Muir-Wood presumed these specimens to be immature and states 'owing to the spirolophus lophophore and the immature form of the loop it is quite impossible to assign *Leptothyris ignota* to any family of the suborder Terebratelloidea' (p. 309). It may be worth examining *Leptothyrella* in relationship to *Malleia*. As far as one can judge from Muir-Wood's descriptions certain similarities exist between the two genera in external features, type of cardinalia and the form of the median septum. The immature form of the loop forms no obstacle to relationship with the Bouchardiinae as the lophophore is unknown for any member of the subfamily.

Malleia Thomson 1927

Malleia Thomson 1927, *N.Z. Board Sci. & Art. Manual No. 7*: 283-4.
Malleia Hatai 1965, *Treatise on Invertebrate Paleontology*, H854-5.
TYPE SPECIES: (Original Designation) *Terebratella portlandica* Chapman 1913.
DIAGNOSIS: Plano-convex Bouchardiinae with hypothyrid foramen and discrete deltidial plates; with the posterior surface of the cardinal process visible as two posteriorly converging pockets; with a median septum which bears two curved lamellae and rudimentary descending branches.
STRATIGRAPHIC RANGE: Oligocene-Pliocene.
DISTRIBUTION: Australia.
COMMENTS: Thomson erected the genus *Malleia* for *Terebratella portlandica* on the basis of its hypothyrid foramen, wide hinge trough and primitive loop. Allan (1940, p. 273) referred the genus to his subfamily Neothyrinae stating that *Malleia* is a primitive member of the group in its foraminal position and loop stage; 'the septum, however, is broadly bifurcating and the hinge-trough long and broad'.

In the following description of the species it is noted that oblique ridges extend between the anterior bases of the socket ridges and the mid-line of the dorsal valve. One of the variable features of the species is the degree of definition of adductor muscle scars. In specimens in which these are well-defined the oblique ridges on the valve floor do not appear as distinct structures but as the posterior borders of the adductor scars. Since the medial limits of these ridges frequently terminate just short of the mid-line of the valve and since the median septum continues as a low ridge beyond their posterior and medial limits, it is unlikely that they could represent the bifurcation of the septum. Since the term 'hinge trough' is defined (Treatise 1965, p. H146) with reference to a bifurcating septum in

association with hinge plates, the lack of either structure in *Malleia* invalidates its use to describe the posterior dorsal valve floor.

Malleia portlandica is described in detail below, because the illustrations of this species in neither Chapman's paper (1913) nor in Thomson's book (1927) give an accurate representation of the disposition of the cardinalia and the septum.

Malleia portlandica (Chapman 1913)
(Pl. 7, fig. 1-6)

Terebratella portlandica Chapman 1913, *Proc. R. Soc. Vict.* 26 (2): 187, Pl. 18, fig. 36a-c, 37, 38.
Terebratella portlandica Chapman 1916, *Rec. Geol. Surv. Vict.* 3 (4): 387, Pl. 65, fig. 36-38.
Malleia portlandica Thomson 1927, *N.Z. Board Sc. & Art*, Manual No. 7: 283-4, fig. 96a-e.

DESCRIPTION: Shell outline subcircular, plano-convex, dorsal valve with short anterior sulcation, ventral valve slightly carinate. Anterior commissure sulcate, lateral commissures rectimarginate, cardinal margin short, slightly curved. Beak ridges subangular, defining short, narrow palintropes. Deltidial plates discrete, small, edging antero-lateral corners of the foramen. Foramen hypothyrid, lined with thin, sessile pedicle collar.

Dorsal valve with strong, straight socket ridges projecting beyond dorsal umbo for approximately one quarter their total length; anteriorly bases of socket ridges confluent with a pair of low ridges extending obliquely in an antero-medial direction to areas just short of mid-line of valve. Cardinal process large, lying between socket ridges and extending from dorsal umbo to points just anterior to mid-length of socket ridges. Ventral surface of cardinal process indented by an inverted V-shaped roughened depression bordered by a rim, this depression appearing to represent the surface of invaginated posterior surface of cardinal process. The cardinal process fused posteriorly with dorsal umbo and laterally with socket ridges but not fused with floor of valve, thus delimiting posterior cave, the roof formed by cardinal process, the sides by socket ridges and the floor by valve floor. Median septum high, wedge-shaped in lateral outline with ventral border slightly longer than attached dorsal border, anterior limit just anterior to mid-length of valve, posteriorly merging with valve floor as low ridge just anterior to hinge platform. Lines of attachment only of lamellar structures attached to septum visible in paratype. However, structures attached to septum apparent in a number of specimens from different localities; these specimens display two curved lamellae, broad at their lines of attachment and narrowing to a point as they curve posteriorly and medially and inserted at approximate mid-height of the septum. Between insertions of lamellae and base of septum two small triangular plates extend from sides of the septum, apparently representing rudiments of descending branches. Adductor muscle impressions, large elongate-ovate scars within which anterior and posterior adductor impressions cannot be separated, anterior limits lying slightly anterior to mid-length

of valve, posteriorly muscles appear to be delimited by low, oblique ridges extending medially from socket ridge bases.

Ventral valve with hinge teeth, strong, rounded and transversely striated, Deep grooves lie immediately beneath hinge teeth for reception of socket ridges. Lateral and posterior walls not thickened. Sessile pedicle collar thin, lining interior of umbo and undersurfaces of deltidial plates. Muscle scars not apparent. Median longitudinal ridge extends from an area level with posterior limits of hinge teeth to a point just posterior to anterior border of valve.

TYPE MATERIAL: Chapman's type material which was used for the above description consists of three specimens, one complete valve and one dorsal and one ventral valve, each obtained from different depths of Mallee Bore No. 11. The holotype P12460 (length 5·5 mm, breadth 5 m, depth 2 mm) was obtained from 160·2-161·54 m (525-530 ft), paratype P12461 (dorsal valve) from 46·93-48·15 m (154-158 ft) and paratype P12462 (ventral valve) from 34·74-45·72 m (114-150 ft). Numbers prefixed 'P' are in the Palaeontological Collection of the National Museum of Victoria.

STRATIGRAPHIC RANGE: Janjukian-Kalimnan.

OCCURRENCE: *South Australia*: *Morgan Limestone* (Balcombian): Between Morgan and Mannum, Murray River. *Dry Creek Sands* (Yatalan): Abattoirs Bore, Adelaide.

Victoria: *Point Addis Limestone* (Janjukian): Aireys Inlet. *Puebla Formation* (Longfordian): Torquay. *Fyansford Formation*: North Belmont Quarry (Batesfordian); Geelong (Bairnsdalian); Warrambine Creek, near Inverleigh (Bairnsdalian). *Muddy Creek Formation* (Balcombian): Clifton Bank, Muddy Creek, Hamilton. *Gippsland Limestone* (Bairnsdalian): Orbost Railway Cutting. *Gambier Limestone* (Bairnsdalian): Portland. *Sandringham Sands-Brighton Group* (Cheltenhamian) Beaumaris. *Bookpurnong Beds* (Cheltenhamian-Kalimnan): Mallee Bores No. 6 34·74-45·72 m (114-150 ft); 46·93-48·15 m (154-158 ft); No. 9 49·68-83·21 m (163-273 ft); No. 10 77·41-90·22 m (254-296 ft); 94·5-97·55 m (310-320 ft); No. 11 153·92-155·28 m (505- 510 ft); 156·97-158·49 m (515-520 ft); 160·2-161·54 m (525-530 ft); 153·92-158·49 m (505-520 ft); 166·11-167·60 m (545-550 ft).

COMMENTS: The holotype (5·5 mm) is smaller in size than the largest specimens (9 mm) obtained from other localities cited above. In addition to the type material, Chapman's Collection of *M. portlandica* is represented in many other Mallee Bores but by only one or two specimens which are rarely complete. Sufficient material from which to gain some idea of the range of variation of the species was obtained from the Abattoirs Bore and Torquay. Features displaying variation are: anterior sulcation (moderate to pronounced), adductor muscle scar impressions (slight to deep) and the extent of the area between the socket ridges occupied by the cardinal process (one half to almost the total length of the socket ridges). In addition the median septum may taper off abruptly posteriorly or it may continue

as a low ridge to a point just beyond the posterior limits of the adductor muscle scars.

Neobouchardia Thomson 1927

Neobouchardia Thomson 1927, *N.Z. Board Sci. & Art.* Manual No. 7: 270-1.
Neobouchardia Allan 1940, *Rec. Canterbury Mus.* 4 (6): 284-5.
Neobouchardia Hatai 1965, *Treatise on Invertebrate Paleontology*, H849.
TYPE SPECIES: (Original Designation) *Bourchardia minima* Thomson 1918.
STRATIGRAPHIC RANGE: Oligocene-Lower Miocene.
DISTRIBUTION: New Zealand (Oligocene-L. Miocene), Australia (Oligocene-L. Miocene).
DIAGNOSIS: Bourchardiinae with a minute epithyrid foramen and fused deltidial plates not delimited within the palintrope; with the cardinalia fused into a solid platform which displays three shallow caves anteriorly and a cardinal process with indented anterior rim; with a small, swollen boss on the septum.

Neobouchardia minima (Thomson 1918)
(Pl. 7, fig. 7)

Bouchardia minima Thomson 1918, *Geol. Mag.* Dec. 6 (5): 260-1, figs. 1a-c.
Bourchardia minima Thomson 1920, *Trans. N.Z. Inst.* 52: 369.
Neobouchardia minima Thomson 1927. *N.Z. Board Sci. & Art,* Manual No. 7: 270-1, figs. 89a-c.
Neobouchardia minima Allan 1932, *Trans. N.Z. Inst.* 63 (1): 16.
Neobouchardia minima Allan 1940, *Rec. Canterbury Mus.* 4 (6): 285.
COMMENTS: Thomson's description (1927, p. 270-1) of the New Zealand members of this species is accurate for specimens found in each of the Australian localities cited below. As Allan (1940, p. 285) states: 'I am unable to separate the Victorian specimens from New Zealand topotypes. I reached this decision reluctantly after a careful comparison of external and internal details, because earlier records of Tertiary brachiopods common to both sides of the Tasman have not hitherto survived critical investigation'. Allan's Victorian specimens were collected from the Scutellina Limestone at Torquay, then the only known locality of *N. minima.*

A considerable effort has been made to find and dissect early ontogenetic stages of *N. minima* in order to display the nature of the hinge platform before excessive thickening of the posterior segment of the shell has taken place. The smallest sizes preserved ranged between 3-4 mm in length and all displayed considerable secondary thickening and a hinge platform of adult pattern.
OCCURRENCE: *New Zealand*: *Kakanui Limestone* (Lower Oligocene): Flat Top Hill; Oamaru, London Creek. *Main Mount Brown Limestone* (Upper Oligo-

cene to Miocene): Middle Waipara and Weka Pass District, Canterbury (type locality).
Victoria: *Point Addis Limestone* (Janjukian): Aireys Inlet. *Jan Juc Formation* (Janjukian): Marl below Point Addis Limestone, Bells Headland, Torquay. '*Scutellina Limestone*' (Longfordian); Jan Juc, Torquay.

ACKNOWLEDGMENTS

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DESCRIPTION OF PLATE 7

All photographs at a magnification of × 8

FIG. 1—*Malleia portlandica* (Chapman), P12460, holotype. Mallee Bore, No. 11, S.A.

FIG. 2—*Malleia portlandica* (Chapman), P12461, paratype, dorsal valve interior.

FIG. 3—*Malleia portlandica* (Chapman), P12462, paratype, ventral valve interior.

FIG. 4—*Malleia portlandica* (Chapman), P12460, holotype, anterior view.

FIG. 5—*Malleia portlandica* (Chapman), P30779, dorsal valve interior showing septal lamellae, Torquay, Victoria.

FIG. 6—*Malleia portlandica* (Chapman), P30780, dorsal valve interior, Abattoirs Bore, Adelaide, S.A.

FIG. 7—*Neobouchardia minima* (Thomson) P30781, dorsal valve interior, Torquay, Victoria.

Abbreviations: **A** = Adductor muscle scar, **B** = Posterior rim of cardinal process, **C** = Anterior rim of cardinal process.

FIG. 8—*Bouchardia rosea* (Mawe) F27471, dorsal valve interior, Rio de Janiero, South America.

Abbreviations: **B** = Posterior rim of cardinal process, **C** = Anterior rim of cardinal process.